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亚洲土著类群硅藻鼠科的演化

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摘要：硅藻鼠科是仅分布于亚洲的啮齿类类群，头骨具豪猪型咬肌结构，下颌则为松鼠型。该类群代表了一个从梳趾鼠类分化出的区域性支系，虽与豪猪次目相近，但并不是它的成员。最早的硅藻鼠化石记录发现于Baluchistan渐新世陆相地层中，稍晚的记录发现于南亚晚渐新世。印度次大陆连续的地层为该科的演化历史提供了主要的化石依据。早中新世晚期至中中新世，硅藻科化石也发现于泰国、中国以及日本。其后的硅藻鼠种类少且鲜有化石记录。晚中新世早期在巴基斯坦有一个种，中国南部晚中新世也可能有一个种。尽管在最早的化石地点发现的标本较多，但其后的时段内除泰国李盆地外化石并不丰富，这指示了其特殊的生活习性或其生活区域化石保存的偏差。已知的化石记录并没有指示出该类群的多样性，也可能是缺少石化作用的结果。硅藻鼠类在水系外围区域延续生存与最近在老挝中部多岩石地带发现的现生*Laonastes*也是一个硅藻鼠的假设相一致。

关键词：中国，巴基斯坦，泰国，西瓦立克堆积，梳趾鼠类，硅藻鼠科

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EVOLUTION OF THE DIATOMYIDAE, AN ENDEMIC FAMILY OF ASIAN RODENTS

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Abstract　The Diatomyidae are a distinctive rodent family of Asian distribution. The skull is characterized by hystricomorphous musculature, and the jaw is sciurognathous in morphology. The group represents a local radiation of ctenodactyloid rodents closely related to, but not a member of Hystricognathi. The fossil record first yields Diatomyidae in the Oligocene terrestrial sediments of Baluchistan, followed by younger occurrences elsewhere in the late Oligocene of southern Asia. Successive deposits of the Indian subcontinent illustrate much of what is known of the history of the family. By the late Early Miocene and Middle Miocene, Diatomyidae are also known from Thailand, China, and Japan. Thereafter, diatomyids are rare and infrequently recorded as fossils. One taxon is known from the early Late Miocene of Pakistan, and there is a possible record in the late Miocene of southern China. Although abundant where found in the oldest fossil sites, diatomyids are not numerous as fossils in later localities, except Li, Thailand. This suggests special habitat preference or bias against preservation at sites where they do occur. The known fossil record does not indicate taxonomic diversity of the group, but this may be an artifact of lack of fossilization. Survival of Diatomyidae as specialized rodents of habitat peripheral to fluvial systems is consistent with the hypothesis that the recently recognized extant *Laonastes* of rocky terrain in central Laos is a diatomyid.

Key words　China, Pakistan, Thailand, Siwaliks, ctenodactyloid rodents, Diatomyidae

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1 Introduction

When Li Chuankui (1974) announced the interesting then-new rodent *Diatomys*, it was clearly derived, but so enigmatic that it defied classification. This rodent from central Shandong Province represented yet another fantastic, presumably endemic, element in the fossil record of China. The dentition was distinctive: strongly bilophodont, four cheekteeth, four roots. Osteological features were in odd combination: Li (1974) noted the sciurognathy, despite the crushed skull of the holotype, and scansorial adaptation of the limbs, and a better-preserved specimen (Dawson et al., 2006) demonstrates hystricomorphy, which was considered a possible condition in 1974. Li (1974) evaluated relationship to Pedetidae and to Geomyoidea (broadly) but hesitated at familial assignment.

Today *Diatomys* and relatives are better known, but systematic affinity is still controversial. Given demonstration of hystricomorphy and discovery of a primitive relative linking *Diatomys* to the Paleogene radiation of ctenodactyloid rodents, *Diatomys* is now seen as a member of a lineage stemming from Asian ctenodactyloids and related to, but not a member of, Hystricognathi. With a large sample of *Diatomys* from Thailand in hand, Mein and Ginsburg (1997) discerned these rodents as members of a distinct Family Diatomyidae.

Subsequently, further records of Diatomyidae have emerged, hinting at moderate diversity in the family. However, these rodents never dominated Asian paleofaunas the way murids and cricetids did at various times, or the way that rhizomyids and sciurids did in many localities, despite low abundance. Apparently only one diatomyid genus occurred in any single locality, and since the Oligocene, usually in low abundance. It is the purpose of this paper to outline the history of Diatomyidae, describe a new Early Miocene taxon, and discuss the distribution through time of the group.

2 Diatomyid fossil record

2.1 *Diatomys* and *Fallomus*

The type locality of *Diatomys shantungensis* is in the Linqu district of central Shandong Province, northern China and south of the Yellow River. Its name is based on its geological occurrence in diatomaceous shale. The type specimen, being a complete individual, although crushed and not well preserved, provides considerable information about this rodent. The dentition is consequently completely represented. Cheek teeth are strongly bilophodont, and moderately high crowned, but not hypsodont. There are four roots, except for the lower premolar, which has three. Premolars are submolariform. Head plus body length being about 250 mm (Li, 1974), this species is relatively large, perhaps a half kilogram in living body mass. These features stand in contrast to most Asian rodents.

Diatomys shantungensis had a broad, if spottily represented distribution. The species is also known from Jiangsu Province in eastern China. East and south of Shandong, on Kyushu Island of Japan, the Sasebo Basin includes early Miocene terrestrial deposits. A locality at Doba has produced a tooth of *D. shantungensis*, and provides a date of 18 ~ 19 Ma (Kato and Otsuka, 1995, who give two dates: 18.9 +/ −2.9 and 18.5 +/ −2.3).

Since the description of the type species, *Diatomys* has been reported elsewhere in Asia. *Diatomys liensis* Mein et Ginsburg (1985) was named for a good sample of isolated teeth from Li Basin, Thailand. Described more fully by the same authors in 1997, the concept of the genus was expanded to include this small form that showed occasional presence of an accessory cusp on lower molars, and the new Family Diatomyidae was created. The age of this locality is somewhat controversial. Initially thought to be late Early Miocene, it is probably middle Miocene in

age (Chaimanee et al., in press). *Diatomys* was reported without description from the early Miocene of Pakistan: the Dalana area of the Zinda Pir Dome (Downing et al., 1993) and the base of the Siwalik section south of Chinji (Flynn, 2000). A similar form is possibly present in the late Early Miocene Manchar Fm. of Sehwan, southern Pakistan (De Bruijn and Hussain, 1984).

A window on the affinity of *Diatomys* was opened by the discovery of a low crowned rodent with four cheek teeth and partial bilophodonty from the Bugti area of Baluchistan. *Fallomus razae* Flynn et al. (1986) was named for a large sample of specimens from Pazbogi Nala, south of Bugti. These fossils showed clear affinity with chapattimyid ctenodactyloids: consistent major cusp locations and connections, large submolariform premolars, large third molars, and retained hypoconulid on lower molars. In addition, whereas *Diatomys* apparently shows no premolar replacement, i. e., the deciduous premolar is retained, *Fallomus* demonstrates the primitive ctenodactyloid condition of normal premolar replacement. *Fallomus* presages the derived bilophodonty of *Diatomys*: opposite cusps joined by transverse crests; suppression of longitudinal crests.

With the discovery of *Fallomus*, it became clear that *Diatomys* was a member of a distinctive lineage derived from the Asiatic ctenodactyloid radiation (see Luckett and Hartenberger, 1985). Flynn et al. (1986) considered *Fallomus* to be early Miocene in age, and considerably older than *Diatomys*-but perhaps around 5 m. y. older in their estimation. Subsequently, French colleagues (Marivaux and Welcomme, 2003) investigated the Bugti area, and located an important small mammal horizon, which recorded multiple species of *Fallomus*. Their research established Oligocene age of these fossils, and they argued for early Oligocene correlation. Reanalysis of paleomagnetic reversal stratigraphy in the Zinda Pir Dome (Lindsay et al. 2005) agrees that *Fallomus* is Oligocene in age; two possible correlations suggest ages of about 28 or 25 Ma, about ten m. y. older than *Diatomys*. Given the apparently long history of Diatomyidae, it seems natural that the fossil record would eventually produce a richer record of its evolution.

2.2 Fossil sequence of the Indian Subcontinent

Fallomus razae occurs in the Chitarwata Formation of western Pakistan, primarily in its type area of Bugti, Baluchistan, and in the vicinity of Dalana village to the east, in the Zinda Pir Dome, westernmost Punjab Province. The localities are near the base of the terrestrial deposits overlying marine sediments, but they are not precisely equivalent in age. In the Dalana region, lower Chitarwata site Z108 is at least 20 m below Z144 (Fig. 1). Near Bugti, the rich locality Paali could be about the same age as the type locality of *F. razae* (Y417), but 2 km separate the sites according to the maps in Flynn et al. (1986) and Marivaux and Welcomme (2003). Whereas Y417 presents one species of *Fallomus*, the rich Paali samples allowed Marivaux and Welcomme (2003) to distinguish new species *F. ginsburgi* and *F. quraishyi* along with *F. razae*. Unlike Y417, all three are present at Z108. Some time depth is represented among these lower Chitarwata sites, and there may be consequent faunal differences, Y417 being older and having one *Fallomus*, the other sites being younger and having several species. Be that as it may, all *Fallomus* in Pakistan is restricted to lower levels of the Chitarwata Fm.

While research advanced in both the Bugti area and the Zinda Pir Dome, Diatomyidae became known in the Kargil district of northern India. The Kargil material was sufficient to name a new species attributed as *Fallomus ladakhensis* Nanda et Sahni (1998). It is derived with respect to *F. razae* (greater crown height and lophodonty). The age of this locality is uncertain, but considered near the Oligocene/Miocene boundary. This species of *Fallomus* was recognized recently in the late Oligocene of Thailand by Marivaux et al. (2004). These finds showed that diatomyids had significant distribution in the mid-Tertiary.

The Oligocene/early Miocene microfossil succession in Pakistan grew more complete with

continued work in both the Zinda Pir Dome and the Siwalik Formations of the Potwar Plateau. Downing et al. (1993) reported superposed small mammal horizons in the Chitarwata and Vihowa formations, and these were discussed more fully by Lindsay et al. (2005), who revised the temporal context (see Fig. 1). Several localities in the upper part of the Chitarwata Fm. produce a distinctive diatomyid that Flynn (in press) describes as a new genus, but one presenting apparent autapomorphies that exclude it as a suitable *Diatomys* ancestor. This diatomyid is, however, closely related to a larger species from the Murree Fm. at Banda Daud Shah (de Bruijn et al., 1981).

In the Potwar Plateau, the family was recorded at the base of the Siwaliks (late Early Miocene) and at a single early Late Miocene locality in the Nagri Formation (Flynn, 2000). The latter diatomyid was named *Willmus* by Flynn and Morgan (2005). The striking fact about these two occurrences in the Siwaliks is the contrasting absence of diatomyids from all other Kamlial, Chinji, and Nagri formation localities.

To complete an outline of the pattern of evolution of the Family Diatomyidae, it is necessary here to pause to describe the scant diatomyids from the Vihowa Fm., Zinda Pir Dome, and the small sample from the base of the Siwaliks in the Potwar Plateau. These specimens, currently in the care of the author, will be housed at the Pakistan Museum of Natural History in Islamabad. Epoxy casts are available at both institutions.

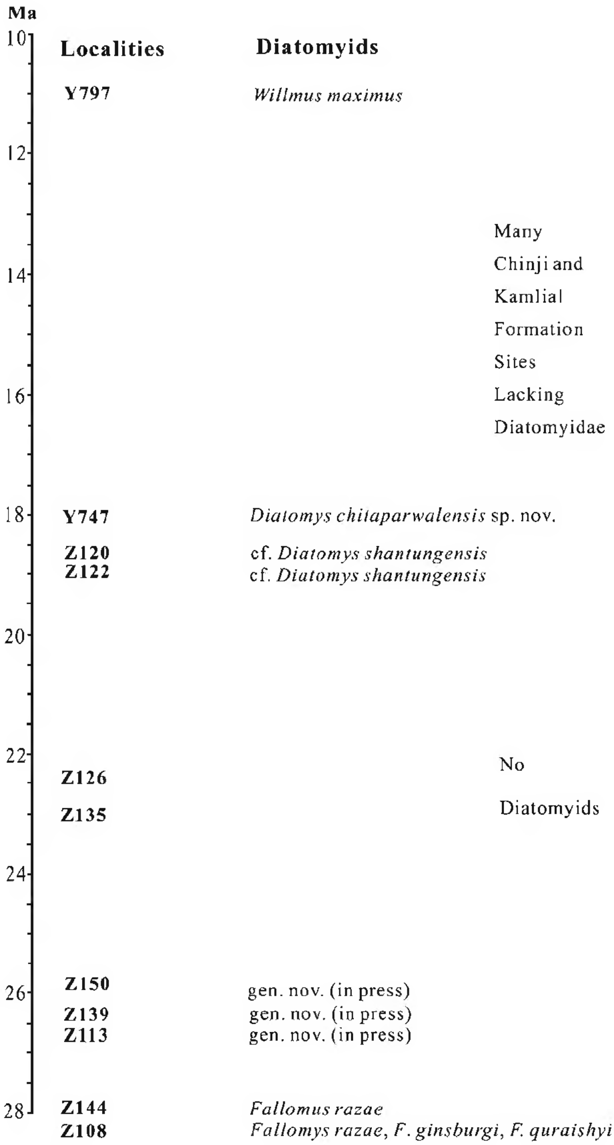

Fig. 1 Temporal distribution of diatomyid localities in the terrestrial record of Pakistan Timescale (Ma) in millions of years Localities are listed to indicate occurrences and to give a sense of absences from most localities; Z prefix for the older sites indicates Zinda Pir Dome, Y prefix indicates Potwar sequence

3 Systematic paleontology

Family DIATOMYIDAE Mein et Ginsburg, 1997

Diagnosis Skull with expanded infraorbital foramen of hystricomorphous structure, sciurognathous mandibular structure, four upper and lower cheek teeth, large low crowned to mesodont molars with four distinct roots, premolars submolariform to molariform and almost as large as molars, cheek teeth are bilophodont and occlusal wear is planar, 3-rooted p4 with triangular anterior lobe based on 3 cusps, incisors with multiserial enamel microstructure, scansorial limb proportions (no postcranial evidence of saltatorial locomotion) (after Mein and Ginsburg, 1997).

Included genera *Diatomys* Li (1974, type genus), *Fallomus* Flynn et al. (1986), *Willmus* Flynn et Morgan (2005), Gen. Nov. (Flynn, in press), ? *Laonastes* Jenkins et al. (2005).

Distribution Oligocene to ? Recent, southern and eastern Asia, from Pakistan and India, through Thailand and South China, to eastern China and Japan, and possibly Laos.

Diatomys Li, 1974

Type species *Diatomys shantungensis* Li, 1974.

Included species *Diatomys shantungensis*, *D. liensis*, and new species described below.

Diagnosis Diatomyid retaining milk teeth (no premolar replacement), lower premolar with indistinct cusps and diminutive remnant of posterior cingulum, squared first and second lower and upper molars (not greatly longer than wide), reduced ectostylid on lower molars, no posteroconid (= hypoconulid) on lower molars, enterostyle on upper molars small to absent, reduced to absent anterior cingulum on upper molars (after Mein and Ginsburg, 1997).

Diatomys cf. *D. shantungensis*

Referred material Two specimens, Z2313, right lower m2 from locality Z124, and Z595, left upper M2 from locality Z122.

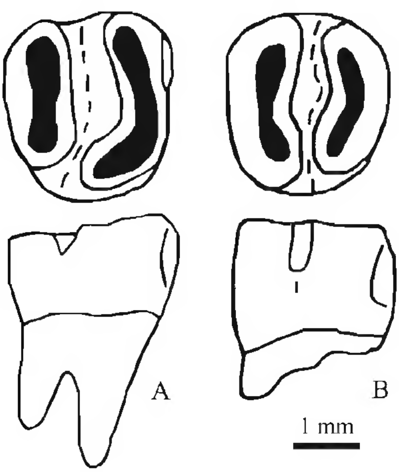

Fig. 2 *Diatomys* molars referred as cf. *D. shantungensis*
A. lower molar Z2313 in occlusal and buccal views; B. upper molar Z595 in occlusal and lingual views

Localities Z124 and Z122 are both in the lower part of the Vihowa Fm., Dalana area of the Zinda Pir Dome, Z122 10 m higher stratigraphically. The localities are correlated to the lower part of Chron 5Er, 19 Ma (Lindsay et al., 2005).

Description Both specimens are strongly bilophodont and of elevated crown height-but they are not hypsodont (Fig. 2). They are quite similar; assignment to tooth position must be taken as hypothetical, but is based on angulation of the crown vs. its roots, and on relative sizes of each loph. Hence, Z2313 is recognized by its anterior loph being transversely longer than the posterior loph, and by having a posterobuccal projection of the anterior loph representing the posterior arm of the protoconid. The buccal side of the tooth is slightly taller than the more worn lingual side. There is a large anterior interdental wear facet and a smaller posterolingual wear facet. This tooth shows no hint of an anterior cingulum, of a hypoconulid, or of an ectostylid. In these features it is completely consist-

ent with *D. shantungensis*. One difference is that the anterior pair of roots is fused, as is the posterior pair of roots.

Roots are broken on Z595. This upper molar is wider than long (Table 1) and less worn than Z2313 (maximum observed crown height: 2.3 mm). This tooth has a nearly planar wear surface, slightly less worn on the buccal side, and showing antero-posterior striations. The shorter posterior loph has a median invagination on its anterior side, clearly demarcating hypocone and metacone. The two lophs converge slightly closer lingually than bucally. There is an anterior interdental wear facet, but none is evident posteriorly.

Discussion These specimens represent a diatomyid population that is very close to, if not conspecific with *Diatomys shantungensis* from the late Early Miocene of China. They correspond in essential features with the hypodigm described by Li (1974), but are somewhat larger. They appear to be perhaps somewhat higher crowned, but this difference is not convincing, being so greatly influenced by wear. Neither tooth is greatly worn, and Z595 is less worn than Z2313, which corresponds to its less pronounced interdental wear facets. Possibly more significant is that the roots are not distinct, but if the specimens represent little-worn, young individuals, then lack of root separation could be a byproduct of immaturity. The age of the Zinda Pir Dome specimens based on paleomagnetic data, ca. 19 Ma, agrees with the fission-track ages for the Japanese record of *D. shantungensis* (Kato and Otsuka, 1995). The Zinda Pir rodent is referred to *D. shantungensis* pending discovery of more complete material.

Diatomys chitaparwalensis sp. nov.

Holotype Yale Geological Survey of Pakistan specimen number YGSP 53256, right m1.

Hypodigm YGSP 53256; 53257 and 53258, right and left m1; 53262, left m2; 53261, ? left m2; 53260, ? M1 fragment; 53259, right M3.

Type locality Y747, base of the Kamlial Formation in the drainage of the Chitaparwala Nala, 18.3 Ma on the Cande and Kent (1995) time scale.

Diagnosis Smaller species of *Diatomys* about the size of *D. liensis* but lower crowned, ectostylid strong on lower molars, double lophs of m1 angled posterolabial-anterolingually.

Etymology Named for the exposures in the upper reaches of Chitaparwala Nala, plus "ensis", latin suffix denoting place. Chitaparwala Nala is the S-N arroyo (nala), south of the village of Qadirpur in the Chinji district; the locality is about 6.5 km south of Qadirpur.

Description Cheek teeth are low crowned (least worn molar, YGSP 53257, is 1 mm high) and mostly well worn, with nearly flat occlusal surfaces. The occlusal wear surface of lower molars is slightly convex mediolaterally, while that of upper molars is slightly concave. Molar size increases posteriorly. All specimens are strongly bilophodont. All show evidence of four roots.

Lower teeth are distinguished by presence of an extra cusp, considered the ectostylid (Fig. 3). Lower molars are squared, not markedly longer than wide as in *Fallomus*, and they lack an anterior cingulum. Lophs are composed of two merged cusps and are inclined weakly anteriorly. The anterior loph of m1 has a large protoconid and a metaconid that forms a distinct bulge in the posterior wall of the anterior loph. Lingual to the metaconid, the anterior loph ends with a backwardly turned marginal crest. The posterior loph includes two cusps as well, the hypoconid and entoconid. A small shelf between the cusps indents the posterior wall of the tooth, but there is no hypoconulid. The posterior loph is indented at the midline both anteriorly and posteriorly. The two lophs are positioned close together; the ectostylid is crowded between them on the buccal side, abutting the protoconid and hypoconid. The less worn YGSP 53257 shows a small metastylid at the lingual end of the anterior loph. The opposed cusps of each loph are not directly transverse, but offset, the buccal cusps posterior to the lingual cusps. This makes the lophs angled with respect to the longitudinal axis of the tooth.

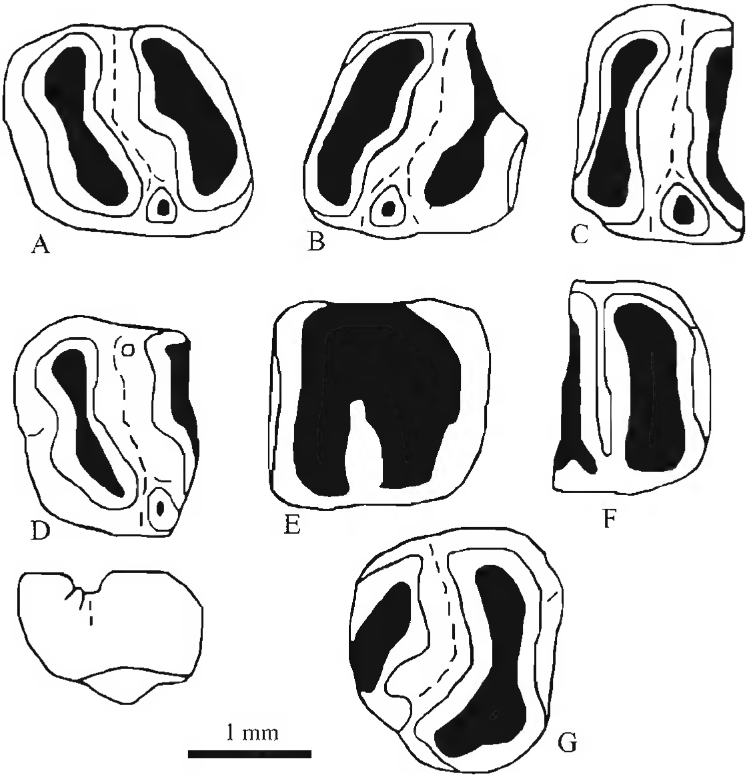

Fig. 3 *Diatomys chitaparwalensis* molars
A ~ C. occlusal views of YGSP 53256 (holotype), 53258, 53262, lower molars all possibly of the same individual; D. YGSP 53257 in occlusal and lingual views; E. YGSP 53261, extremely worn lower molar; F. YGSP 53260, upper molar fragment; G. YGSP 53259, right M3

YGSP 53262, broken anteriorly, represents m2. It is similar to m1, but is wider (Table 1) and does not show strong angulation of the lophs. The ectostylid is relatively larger than in m1. YGSP 53261 could represent another highly worn m2.

Table 1 Measurements of *Diatomys*: cf. *D. shantungensis* and *D. chitaparwalensis* sp. nov.

	Specimen Number	Molar	Length	Width
cf. *D. shantungensis*	Z2313	m2	2.9	3.1
	Z595	M2	2.6	3.1
D. chitaparewalensis	YGSP53256	m1	2.2	1.9
	YGSP53258	m1	2.0	2.0
	YGSP53257	m1	—	2.0
	YGSP53262	m2	—	2.2
	YGSP53261	m2?	2.0	2.1
	YGSP53260	? M	—	1.9
	YGSP53259	M3	1.9	2.2

YGSP 53260, broken and worn, shows two simple transverse lophs. It is taken as an upper molar largely because its wear is gently concave instead of convex. It is narrower than M3, about the width expected of M1. A cuspule between the major lophs is possibly indicated by a low,

marginal expansion of the dentine; homology being uncertain, this could be in the position of an enterostyle or a mesostyle.

M3 is transversely wider than long. Its prominent anterior loph is composed of a large, transversely-oriented paracone and posteriorly-turned protocone. The posterior loph is short and buccal in position, being derived from a large, transverse metacone and minute hypocone. The lightly worn hypocone abuts the posteriorly extended protocone. Paracone and metacone are well separated. Despite breakage, the root under the protocone appears largest, that under the hypocone is reduced, and the small roots under paracone and metacone are appressed.

Discussion These specimens are lophodont and, despite low crown height, quickly develop a tooth crown pattern of two transverse loops. For example, the least worn specimen, YGSP 53257, shows merged cusps although not much of the cusp tips has been removed by wear. Several specimens show the same degree of advanced wear (Fig. 3A ~ C) and may have originated from the same individual.

The basal Siwalik diatomyid represents a new species of *Diatomys* that is smaller and lower crowned than *Diatomys shantungensis*, and it retains an ectostylid, a feature that can be interpreted as primitive. The early Siwalik species is apparently derived in having oblique lophs, at least on m1. *Diatomys chitaparwalensis*, sp. nov., resembles *D. liensis* of Thailand in size and in retention of an ectostylid, which is found occasionally in the latter. However, *D. liensis* is the highest crowned of known *Diatomys* species, and is derived in its reduced premolars. It is also, apparently, the youngest known *Diatomys*.

Diatomys chitaparwalensis, sp. nov., is accommodated in the genus *Diatomys* because it is strongly bilophodont, with squared molars and no cingulae. It is clearly derived in these features beyond *Fallomus* and the new genus under study from the upper part of the Chitarwata Fm. (Fig. 1). It is much smaller and lower crowned than *Willmus* Flynn et Morgan (2005). Both *Diatomys shantungensis* and *D. liensis* are higher crowned than *D. chitaparwalensis*, and both show reduction of ectostylids, although *D. liensis* has the ectostylid in a minority of individuals. *D. chitaparwalensis* presents primitive features of low crown height and a strong ectostylid, but is derived in its oblique lophs on m1, unlike the apparently contemporary *D. shantungensis* lineage.

4 Discussion and conclusions

The Diatomyidae are sporadically represented in the fossil record. Fig. 1 presents the record for terrestrial deposits in Pakistan for which we have paleomagnetic control. Older localities with a Z prefix are from the Zinda Pir Dome, and as noted above, this figure presents the older of two age interpretations for these localities. Sites with a Y prefix are from the Potwar Plateau, in this case the Chinji and Nagri areas. Paleomagnetic data are not yet developed for the deposits of Dera Bugti. Sites there yield *Fallomus*, and these could antedate the Zinda Pir sites slightly, but the same species occur in both areas.

The oldest Zinda Pir site yielding *Fallomus*, Z108, is given an early (or possibly late) Oligocene age by Lindsay et al. (2005). Younger deposits (Z113, 139, 150) yield a different diatomyid that is clearly derived with respect to *Fallomus*. A number of younger, productive sites (e.g., Z135, Z126) lack diatomyids. Near the top of the Zinda Pir section, two specimens represent derived *Diatomys*. These antedate somewhat the base of the Potwar sequence. The oldest Potwar locality Y747, in the base of the terrestrial deposits and considered Kamlial Fm., yields a small sample of teeth that represent a quite different species of *Diatomys*. This form, *Diatomys chitaparwalensis* sp. nov., did not develop the higher crown and simplified bilophodonty of *D. shantungensis*. Above Y747 are many localities throughout the Kamlial, Chinji, and younger formations. Only one, Nagri locality Y797 at about 11 Ma, produces a diatomyid. This large, high crowned species is *Willmus maximus*.

There are other diatomyid records, but not many fossils. As noted above, *Fallomus* has been found in Thailand and Kargil, India. Other forms have been noted at Banda Daud Shah and Sehwan in Pakistan, but there are few specimens of each. The type species of *Diatomys* occurs in the early Miocene of Shandong and Jiangsu, China, and Sasebo, Japan, very few specimens in total. *Diatomys liensis* from the Li Basin, middle Miocene of Thailand, is represented by a large sample.

The pattern of preservation of Diatomyidae is intriguing. *Fallomus* in Pakistan is abundant at small mammal sites. The Z113 diatomyid is also a common element. Thereafter in the Siwaliks, however, diatomyids are either rare-or absent. Other records in Asia are generally poor, the exception being the large Li Basin sample of *Diatomys*. The pattern suggests preference for a particular habitat, in contrast to most other known fossil rodents that seem widespread. Most Siwalik lineages, for example, appear to be nearly ubiquitous, co-occurring in multiple and successive sites (Barry et al., 1995, 2002). The paleoecology of the lower part of the Chitarawata Formation apparently presented favorable habitat, as did Li Basin, Thailand, and the diatomyids at these sites are abundantly preserved. In Pakistan, Miocene diatomyid records became spotty-as if the family was not successful, but existed peripherally to the areas of deposition, and was recorded only when opportunity arose. Possibly the habitat preference of the diatomyids changed through time. Perhaps diatomyids were not successful after the Oligocene in the moist, subtropical conditions of most of the Indian subcontinent. They possibly survived as rodents adapted to marginal conditions away from the depositional setting. This implies upland, well-drained habitat out of the floodplains.

As to pattern of evolution, the fossil record is so limited that until now, it was possible to conceive of one evolving line of Diatomyidae. This was characterized by size increase, simplification of occlusal surfaces, and development of extreme bilophodonty with moderately increased crown height. However unlikely this may seem, it is a parsimonious scenario-and now it can be rejected, in part. Quite clearly, *Diatomys shantungensis* or a form close to it was present in the late Early Miocene of Pakistan, coeval with the different *Diatomys chitaparwalensis* that retained an ectostylid and remained brachydont. Further, as Mary Dawson counsels (All the World's a Stage for Evolution Symposium, Powdermill, 2005), the apparent low diversity and simple pattern of diatomyid evolution may simply be a function of the poor fossil record.

So, what happened to Diatomyidae? The latest record of Diatomyidae formally recognized is *Willmus maximus*, early Late Miocene. It is a unique record, possibly reflecting marginal habitat, unusual for the subtropical Siwaliks. It is tempting to see the diatomyids as a group that shifted to drier habitat. Also possibly Diatomyidae persisted, unrecognized, in some faunas. An example is a high crowned, bilophodont rodent in the late Miocene of Leilao, Yunnan. Ni and Qiu (2002) hypothesized that this poorly represented taxon could be a pedetid-but it seems also possible that it is a late-surviving diatomyid.

Early last year came the astonishing announcement of a new family of rodents from Laos. *Laonastes* Jenkins et al. (2005) was named for an extant rodent just recently recognized in the Khammouan Limestone National Biodiversity Conservation Area of central Laos. It is hystricomorphous but not hystricognathous, and moderatley high crowned and bilophodont. Possibly this represents a surviving diatomyid, but that idea requires further testing undertaken by Dawson et al. (2006). Interestingly, it is a member of a mammalian community inhabiting forested karstic terrain, rocky and with a seasonal shortage of moisture (Musser et al., 2005). Could *Laonastes* be just the sort of rodent presaged by *Willmus*? This envisions a moderately high crowned herbivore adopting a habitat (rocky terrain) quite different from the hypothetical moisture-dependent, floodplain habitat of *Fallomus*.

This idea is testable by continued research on the living *Laonastes*, on the Pleistocene fossil record of Southeast Asia, and on the Neogene small mammal fossil record throughout south-

ern Asia. Regardless of the affinity of *Laonastes*, the fossil record of Diatomyidae has proven difficult to recover. Diatomyidae, at least later species, are an example of specialized small mammals infrequently encountered in any habitat, and less frequently found in the fossil record. Their rarity as fossils may reflect accurately their infrequent occurrence in censuses of living communities.

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References

Barry J C, Morgan M E, Flynn L J et al., 1995. Patterns of faunal turnover and diversity in the Neogene Siwaliks of northern Pakistan. Palaeogeogr, Palaeoclimatol, Palaeoecol, **115**: 209 ~ 226

Barry J C, Morgan M E, Flynn L J et al., 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. Paleobiol Mem, **3**: 1 ~ 71

Cande S C, Kent D V, 1995. Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. J Geophys Res, **100**B: 6093 ~ 6095

Chaimannee Y, Yamee C, Marandat B et al. (in press). First microvertebrates from the middle Miocene intermontane Mae Moh Basin (Thailand): Biochronological and paleoenvironmental implications. Bull Carnegie Mus Nat Hist

Dawson M R, Marivaux L, Li C et al., 2006. *Laonastes* and the "Lazarus Effect" in Recent mammals. Science, **311**: 1456 ~ 1458

De Bruijn H, Taseer Hussain S, 1984. The succession of rodent faunas from the lower Manchar Formation, southern Pakistan, and its relevance for the biostratigraphy of the Mediterranean Miocene. Paléobiologie Continentale, Montpellier, **14**(2): 191 ~ 204

De Bruijn H, Taseer Hussain S, Leinders J J M, 1981. Fossil rodents from the Murree formation near Banda Daud Shah, Kohat, Pakistan. Proc K Ned Akad Wet, Ser B, **84**(1): 71 ~ 99

Downing K F, Lindsay E H, Downs W R et al., 1993. Lithostratigraphy and vertebrate biostratigraphy of the Early Miocene Himalayan Foreland, Zinda Pir Dome, Pakistan. Sediment Geol, **87**: 25 ~ 37

Flynn L J, 2000. The great small mammal revolution. Himalayan Geol, **21**: 39 ~ 42

Flynn L J (in press). Origin and evolution of the Diatomyidae, with clues to their paleoecology from the fossil record. Bull Carnegie Mus Nat Hist

Flynn L J, Jacobs L L, Cheema I U, 1986. Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. Am Mus Novit, (2841): 1 ~ 58

Flynn L J, Morgan M E, 2005. An unusual diatomyid rodent from an infrequently sampled late Miocene interval in the Siwaliks of Pakistan. Palaeontologica Electronica, **8**(1) 17A: 10 p., 309KB; http:palaeo-electronica.org/toc.htm

Jenkins P D, Kilpatrick C W, Robinson M F et al., 2005. Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hystricognatha) from Lao PDR. Syst Biodiv, **2**(4): 410 ~ 454

Kato T, Otsuka H, 1995. Discovery of the Oligo-Miocene rodents from west Japan and their geological and paleontological significance. Vert PalAsiat(古脊椎动物学报), **33**(4): 315 ~ 329

Li C K (李传夔), 1974. A probable geomyoid rodent from Middle Miocene of Linchu, Shantung. Vert PalAsiat (古脊椎动物学报), **12**(1): 43 ~ 53 (in Chinese with English summary)

Lindsay E H, Flynn L J, Cheema I U et al., 2005. Will Downs and the Zinda Pir Dome. Palaeontologia Electronica, **8**(1) 19A: 19pp., 1MB; http:palaeo-electronica.org/toc.htm

Luckett W P, Hartenberger J L, 1985. Evolutionary relationships among Rodents: Comments and Conclusions. In: Luckett W P, Hartenberger J L eds. Evolutionary relationships among rodents: A multidisciplinary analysis. New York and London: Plenum Press. 685 ~ 712

Marivaux L, Chaimanee Y, Yamee C et al., 2004. Discovery of *Fallomus ladakhensis* Nanda & Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Phetchaburi Province, Thailand): systematic, biochronological and paleoenvironmental implications. Geodiversitas, **26**(3): 493 ~ 507

Marivaux L, Welcomme J-L, 2003. New diatomyid and baluchimyine rodents from the Oligocene of Pakistan (Bugti Hills, Balochistan): Systematic and Paleobiogeographic implications. J Vert Paleont, **23**: 420 ~ 434

Mein P, Ginsburg L, 1985. Les rongeurs miocènes de Li (Thaïlande). Compte Rendus Acad Sci, Paris, Sér 2, **301**: 1369 ~ 1374

Mein P, Ginsburg L, 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: systematique, biostratigraphie et paléoenvironnement. Geodiversitas, **19**: 783 ~ 844

Musser G G, Smith A L, Robinson M F et al., 2005. Description of a new genus and species of rodent (Murinae, Muridae, Rodentia) from the Khammouan Limestone National Biodiversity Conservation Area in Lao PDR. Am Mus Novit, (3497): 1 ~ 31

Nanda A C, Sahni A, 1998. Ctenodactyloid rodent assemblage from Kargil Formation, Ladakh Molasse Group: Age and paleobiogeographic implications for the Indian subcontinent in the Oligo-Miocene. Geobios, **31**(4): 533 ~ 544

Ni X, Qiu Z, 2002. The micromammalian fauna from the Leilao, Yuanmou hominoid locality: Implications for biochronology and paleoecology. J Hum Evol, **42**: 535 ~ 546